Anatomy and phylogeny of the cyprinid fish genus *Onychostoma* Günther, 1896

CHEN YIYU

Institute of Hydrobiology, Academia Sinica, Wuhan, China

CONTENTS

INTRODUCTION

Onychostoma Günther, 1896 (type species, *Onychostoma laticeps* Günther= *Barbus simus* Sauvage & Dabry, 1874) is a cyprinid fish genus having its distribution in eastern Asia and is characterized primarily by a broad, inferior mouth with a cornified cutting edge. Since this, so-called 'sector mouth' is also a feature which supposedly characterizes *Varicorhinus* Rüppell, many authors (Nichols, 1925, 1928, 1943; Lin, 1933; Fang, 1940; Wu *et al.*, 1977) have regarded it as a synonym of that genus (type species *Varicorhinus beso* Rüppell). Although Bănărescu (1971) and Taki (1975) have recognised the independent nature of *Onychostoma*, they did not explore the relationship between *Varicorhinus* and *Onychostoma*. Howes (1982) studied the anatomy and evolution of the jaws in 'sector mouth' fishes, including the genera *Cyprinion*, *Varicorhinus*, *Capoeta* and *Onychostoma*. Howes concluded 'in this study the presence of a sector mouth in various cyprinid taxa is seen both as a character indicating relation-ship (synapomorphy) and as one independently evolved as a parallelism'. The existence of synapomorphic osteological and myological characters indicate *Cyprinion* as a mono-phyletic group, but '. . . the phyletic relationship of *Onycho-stoma*, *Varicorhinus* and *Capoeta* have yet to be determined' (Howes, 1982:320 & 333).

Bănărescu (1971) divided *Onychostoma* into two subgenera, *Onychostoma sensu stricto* and *Scaphesthes* Oshima, 1919 (type species: *Scaphesthes tamusuiensis* Oshima = *Gymno-stomus barbatulus* Pellegrin, 1908). Taki (1975) considered *Onychostoma* closely related to *Semiplotus*, *Scaphiodonichthys*, *Scaphiodon* and *Scaphiognathops*, and recognised these genera as an '*Onychostoma*-group'. He also divided *Onycho-stoma* into two subgenera, *Onychostoma* and *Gymnostomus* Heckel, 1842 (type species: *Gymnostomus ariza*). Wu *et al.*

(1977) included *Onychostoma* and *Scaphesthes* as subgenera in the composite genus *Varicorhinus*. They also included some species of *Scaphiodonichthys* in the subgenus *Onycho-stoma*. Howes (1982) included *Semiplotus* and *Scaphio-donichthys* in the genus *Cyprinion*. None of those authors have established the monophyly of *Onychostoma*, let alone its phylogenetic relationship.

There are presently recognised 14 species in the genus *Onychostoma* (including *Scaphesthes*). A detailed anatomical study of eight species is reported in this paper. The informa-tion gained from this study has provided a basis for a discussion of the classification and relationships of *Onycho-stoma*. I regard the genus *Onychostoma* as belonging to the barbin subgroup of the subfamily Cyprininae *sensu* Howes (1987) (= subfamily Barbinae *sensu* Chen *et al.*, 1984). From this standpoint the phyletic relationships between *Onycho-stoma* and related genera may be discussed.

METHODS AND MATERIALS

The osteology was studied from alcian-alizarin stained speci-mens and dry skeletal preparations. Some characters have been examined using dissected specimens.

ABBREVIATIONS. BMNH, British Museum (Natural History); IHAS, Institute of Hydrobiology, Academia Sinica. A = alizarin stained preparation; D = dissected specimen; S = dry skeleton. All specimens are deposited in the British Museum (Natural History).

Acapoeta tanganica (= *Varicorhinus tanganica*) BMNH 1955. 12. 10: 881 (D); 1906. 9. 6: 11 (S); *Barbus barbus* BMNH uncat. (S); *B. bowkeri* BMNH 1962. 8. 28: 8 (S); *B. bynni* BMNH 1861. 9. 9: 65 (S); *B. callensis* BMNH 1869. 1. 29: 4 (S); *B. gregorii* BMNH 1893.12. 2:

36 (S); *B. longiceps* BMNH 1864. 8. 20: 21 (S); *B. luteus* BMNH 1874. 4. 28: 23 (S); *B. oxyrhynchus* BMNH 1906. 8. 25: 17 (S); *B. rocadasi* BMNH 1911. 6. 1: 26 (S); *Capoeta capoeta* BMNH 1968. 12. 13: 405–416 (A, D); 1906. 9. 6: 11 (S); *C. trutta* BMNH 1974. 2. 22: 1374–1377 (D); *Cirrhina jullieni* BMNH 1883. 7. 4: 47 (S); *Cyprinion macrostomus* BMNH 1974. 2. 22: 1177–1179 (A, D); *C. watsoni* BMNH 1889. 2. 1: 379 (D); *Garra quadrimaculatus* BMNH 1902. 12. 13: 420 (S); *Labeo ariza* (= *Gymnostomus ariza*) BMNH 1889. 9. 26: 82 (D); *L. cylindricus* BMNH 1902. 5. 26: 23 (S); *L. niloticus* BMNH unregistered (S); *Onychostoma gerlachi* BMNH 1988. 6. 24: 23–5 (ex. IHAS 66.249 & 261; A, D); *O. lini* BMNH 1988. 6. 24: 13 (ex. IHAS76.IV.6809, D); *O. rhomboides* BMNH 1988. 6. 24: 14–16 (ex. IHAS 58.7.284, 285; A, D); *O. sima* (= *O. laticeps*) BMNH 1969. 4. 15: 110 (S); 1988. 6. 24: 1–3 (ex. IHAS 81. IV. 791, 792; D, A); *Scaphesthes barbatulus* BMNH 1988. 6. 24: 17–19 (ex. IHAS 74. VI. 844, 931; A, D); *S. barbatus* BMNH 1988. 6. 24: 7–12 (ex. IHAS 75. IV. 2439, 440, 270; D, A, A); *S. lepturus* BMNH 1988. 6. 24: 20–22 (ex. IHAS 76. V. 9379, 5085; D, A); *S. macrolepis* BMNH 1988. 6. 24: 4–6 (ex. IHAS 82. V. 2307, 2399; D, A); *Scaphiodonichthys acanthopterus* BMNH 1988. 6. 24: 26–28 (ex. IHAS 78. V. 383, 489; D, A); *Sc. burmanicus* BMNH 1893. 2. 16: 32 (S); 1980. 12. 17: 113–4 (D); *Sc. macracanthus* BMNH 1988. 6. 24: 29 (ex. IHAS 64. 4. 8; D); *Schizothorax prenanti* BMNH 1969. 4. 15: 120 (D); *Sch. richardsoni* BMNH 1881. 9. 2: 85–7 (D); *Semiplotus semiplotus* BMNH 1889. 2. 1: 364 (D); 1889. 2. 1: 369 (S); *Varicorhinus altipinnis* BMNH 1975. 9. 5: 18–19 (D).*V. beso* BMNH 1902. 12. 13: 365–370 (A. D); 1902; 12. 13: 377 (S); *V. macrolepidotus* BMNH 1976. 5. 21: 12–13 (D); *V. maroccanus* BMNH 1972. 9. 13: 1–3 (D); *V. nyassensis* BMNH 1974. 1. 15: 110 (D); *V. ruwenzorii* BMNH 1971. 1. 5: 154–175 (D).

Abbreviations used in the figures

Aa	Anguloarticular
Am	*Adductor mandibulae* muscle
Bo	Basioccipital
Bp	Basioccipital process
Cm	Coronomeckelian bone
Cp	Coronoid process of dentary
De	Dentary
Do	*Dilatator operculi* muscle
Epi	Epioccipital
Exo	Exoccipital
Fr	Frontal
Fsef	Frontal-supraethmoid foramen
Ic	Intercalar
Io	Infraorbitals (numbered)
Lap	*Levator arcus palatini* muscle
Le	Lateral ethmoid
Lo	*Levator operculi* muscle
Me	Mesethmoid
Mp	Masticatory plate
Mx	Maxillary
Nc	Neural complex
Ns	Neural spines
Of	Olfactory foramen
Op	Operculum
Os	Orbitosphenoid
Pal	Palatine
Par	Parietal
Pe	Preethmoid
Pmp	Postero-medial process of symphysial surface of dentary
Pmx	Premaxillary
Pro	Prootic
Ps	Parasphenoid
Pte	Pterotic
Ptf	Posttemporal fossa
Pts	Pterosphenoid
Pty	Pterygiophore (dorsal)
Se	Supraethmoid
Sg	Snout groove
Sj	Synarthritic mandibular joint
Sn	Supraneurals (numbered)
So	Supraoccipital
Sor	Supraorbital
Sp	Sphenotic
Srp	Supraethmoid rostral process
Stf	Subtemporal fossa
Vo	Vomer
Vf	Vomer facet

ANATOMICAL CHARACTERS AND THEIR PHYLOGENETIC SIGNIFICANCE

Cranium

The neurocranium of *Onychostoma sima* is shown in Fig. 1. In general appearance the cranium of *Onychostoma* and *Scaphesthes* is broad and slightly depressed. The posterior part of the cranium (occipital region) is short, being less than one-third of total cranial length. This condition is also found in *Cyprinion*, *Semiplotus* and *Scaphiodonichthys* but in these taxa, the occipital region is even shorter. In *Varicorhinus* and *Capoeta* the neurocranium is more or less narrow and elongate (Fig. 2); its posterior (occipital) part is almost a half the total cranial length, which is regarded as plesiomorphic for cyprinid fishes.

In *Onychostoma sima* (Fig. 1 & Fig. 3), the supraethmoid is broad and short with a medial anterior process. This rostral process is directed ventrally and forms a vertical strut. The medial part of the supraethmoid is deeply depressed and covered with a thick connective tissue. The kinethmoid is rod-shaped and lies along the medial depression of the supra-ethmoid. The mesethmoid is very short and hardly protrudes beyond the anterior border of the supraethmoid. Antero-ventrally the mesethmoid forms a surface that provides part of the preethmoid fossa. The notched posterior border of the mesethmoid forms part of the olfactory foramen. There are two pairs of preethmoids in *Onychostoma sima*, a condition comparable to that in *Cyprinus*; a thick cartilage pad separates the preethmoid and the maxillary process. Each well-developed lateral ethmoid (Fig. 4a) forms a triangular wall, the ventral border of which is almost on the same horizontal level as the vomer. It is more or less compressed and has only a moderately-developed facet articulating with the entoptery-goid. The palatine (Fig. 5a) is short and compressed, its antero-ventral process articulates directly with the vomer. The vomer (Fig. 1 & Fig. 6a) is short, its posterior margin extending to a line level with that of the lateral ethmoid walls; anteriorly it curves ventrad and has a slight transverse convexity. Antero-laterally it is produced into a wedge-shaped platform which provides the lower part of the preeth-moid fossa. Below the preethmoid there is a small facet (Fig. 6a, Vf) into which articulates the palatine.

In all species of *Onychostoma* and *Scaphesthes*, whether the mouth is wide or narrow (see below), the condition of the ethmo-vomerine region is structurally the same as in *Onycho-stoma sima*. *Cyprinion*, *Semiplotus* and *Scaphiodonichthys* also possess a broad supraethmoid with ventrally directed rostral process. In *Semiplotus semiplotus* and *Scaphiodonich-thys burmanicus*, the supraethmoid is very short and almost vertically aligned. There is a foramen between the frontals and the supraethmoid (Howes, 1982). In the wide-mouth species of *Onychostoma*, *Scaphesthes* and in the other taxa mentioned the palatines are more compressed (Fig. 5b,c). The vomers are more or less hypertrophied with a flat anterior border; all species of these taxa possess a facet with
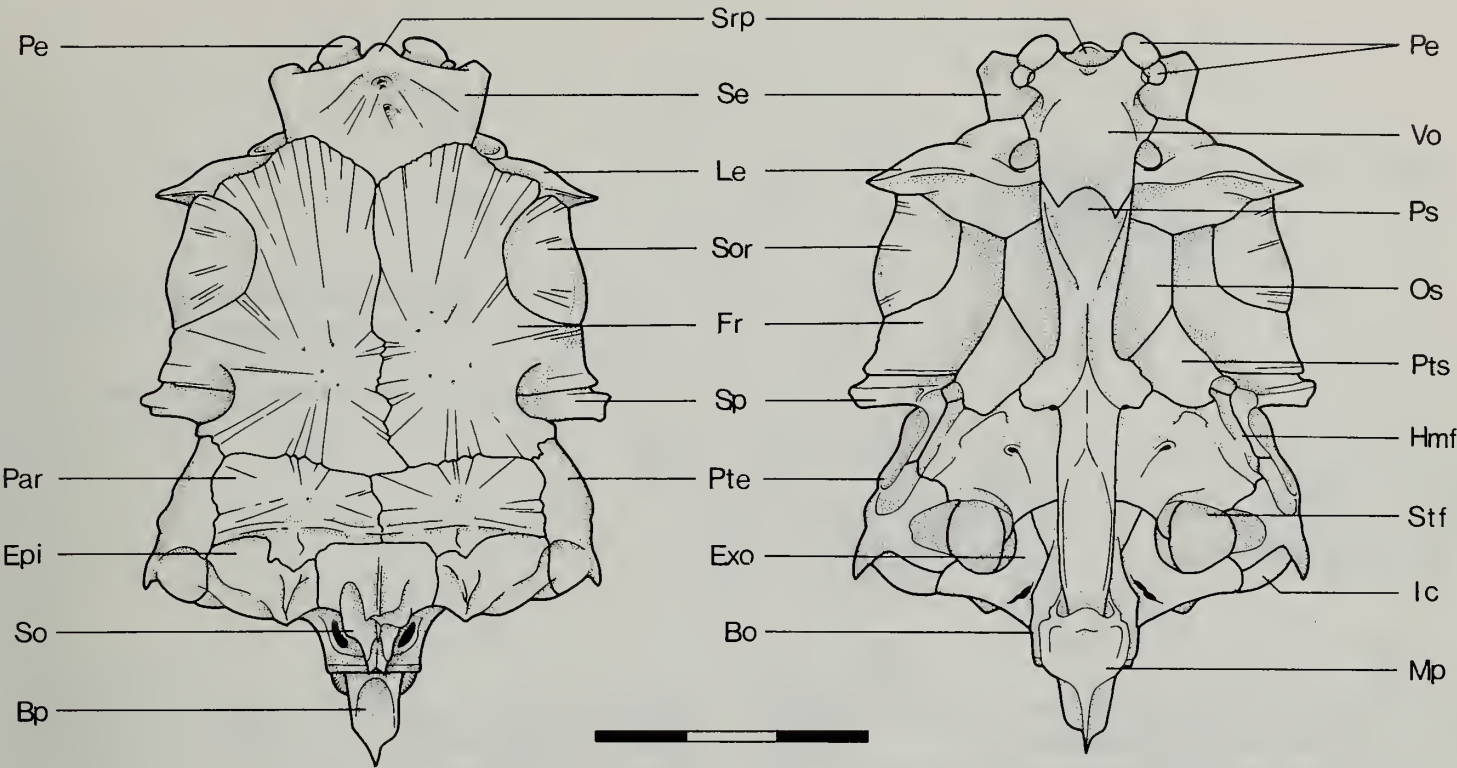
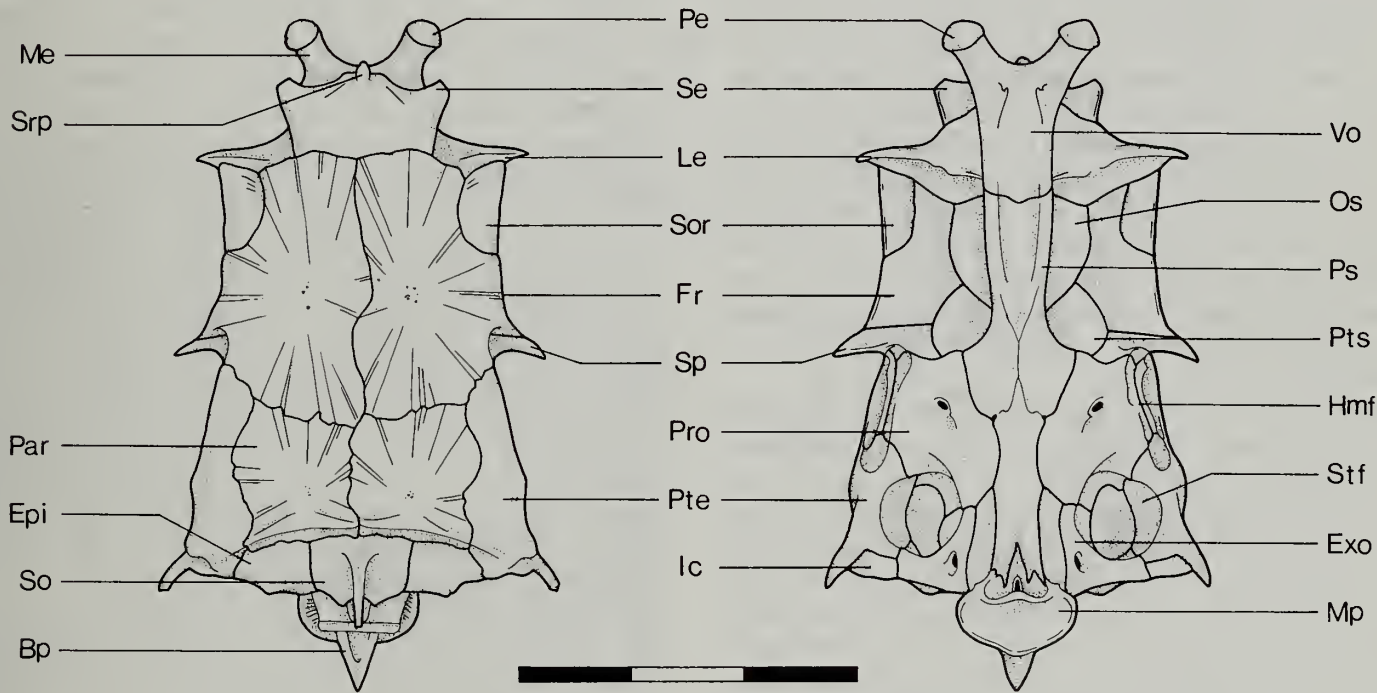**Fig. 1** Neurocranium of *Onychostoma sima* in dorsal (left) and ventral (right) views

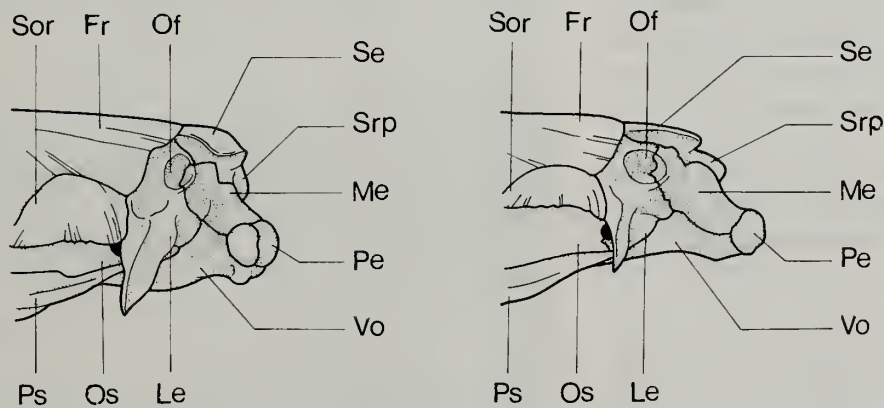**Fig. 2** Neurocranium of *Varicorhinus beso* in dorsal (left) and ventral (right) views

Fig. 3 Ethmo-vomerine regions in lateral view:
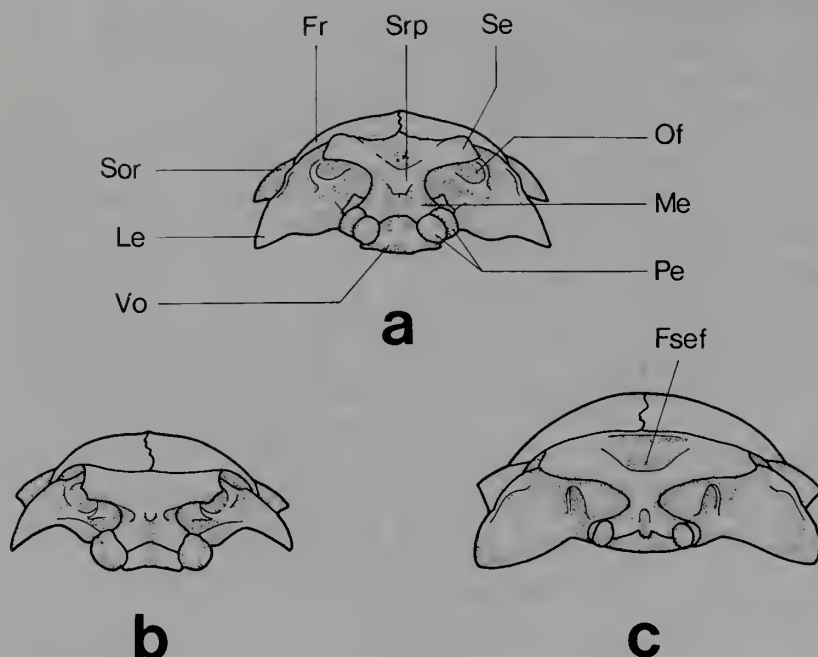(left) *Onychostoma sima*
(right) *Varicorhinus beso*

Fig. 4 Neurocranium in anterior view:
  a. *Onychostoma sima*
  b. *Varicorhinus beso*
  c. *Scaphiodonichthys burmanicus*

which articulates the palatine; in some, such as *Semiplotus semiplotus*, the facet is well-developed.

In *Varicorhinus beso* (Fig. 2 & Fig. 3) the supraethmoid is broad with a small medial anterior process. The rostral process is directed anteriorly. Compared with *Onychostoma* the mesethmoid is slightly longer and protrudes anteriorly below the supraethmoid; the vomer is V-shaped, thinner and laterally it forms a wedge-shaped platform which provides the lower part of the preethmoid fossa. The anterior border of the vomer and the mesethmoid are concave and bear a wide groove to accommodate the rod-shaped kinethmoid. The ventral surface of the vomer lacks a palatine articulatory facet, but bears two small process on either side of the midline to which the palatine ligament attaches. In contrast to *Onychostoma* the lateral ethmoid wings have a concave ventral margin, lie above the horizontal plane of the vomer and are thinner (Fig. 4b).

No distinct differences have been found in the *orbital region* between *Onychostoma*, *Varicorhinus*, *Cyprinion*, *Scaphesthes*, *Scaphiodonichthys* and *Semiplotus*. In these genera the frontals are all broad; the supraorbital bones are large; the orbitosphenoids are deep and ventro-medially they are joined to form a thick interorbital septum which contacts the parasphenoid. The pterosphenoids provide the walls of the optic foramen and the anterior part of the posterior myodome. Posteriorly each pterosphenoid is bordered by the sphenotic and the prootic and does not contact the ascending wing of the parasphenoid. The parasphenoid is horizontally aligned; anteriorly it narrows, then widens and becomes concave where it overlies the vomer; posteriorly each broad ascending wing contacts the respective prootic. The midline ridge of the parasphenoid is well-developed in most species of the above named genera, but in a few (e.g. *Cyprinion watsoni*) it is not distinct.

The *otic region* is short in *Onychostoma* (Fig. 1), *Scaphesthes*, *Scaphiodonichthys*, *Semiplotus* and *Cyprinion*. The parietals and the prootics are short, deep and almost rectangular. Each sphenotic projects laterally as a spinous or broad ledge, at the ventral base of which there is a large depression which forms the antero-lateral part of the hyomandibular fossa. The prootic forms the lateral boundary of the anterior hyomandibular fossa and the anteromesial boundary of the sub-temporal fossa. The subtemporal fossa is deep with an anterior cavity; its outline is elliptical, with the long axis transverse. The inner wall of the fossa is formed by the prootic, and the outer by the pterotic; the posterior wall by the pterotic and the exoccipital; the epioccipital forms the roof of the fossa. The pterotic is short and broad; antero-ventrally it houses the greater portion of the posterior hyomandibular fossa. Its ventromedial surface contains the outer part of the subtemporal fossa, which forms a U-shaped depression, and its dorsal surface forms the lateral wall of the posttemporal fossa. In *Onychostoma*, *Scaphesthes*, *Scaphio-donichthys* and *Semiplotus*, the posttemporal fossae (Fig. 7 a, b) are very deep, the anterior border of the fossa extends almost to the frontal. In these taxa the roof of the posttem-poral fossa is formed by the parietal and the medial wall from the exoccipital. However, in *Cyprinion* (Fig. 7d) the post-temporal fossae are shallower and open into the subtemporal fossae; the parietals contribute only a small portion anteriorly to the posttemporal fossae. Although the basioccipital (masti-catory) plate is entirely absent in *Scaphiodonichthys bur-manicus* (Howes, 1982), the ventral surface of the pharyngeal process is expanded into a triangular masticatory plate in all species of *Onychostoma* and *Scaphesthes*, and in *Scaphio-donichthys acanthopterus* and *S. macracanthus*.

In contrast to the above cited genera *Varicorhinus beso* (Fig. 2) has a square parietal, an elongate prootic and a circular subtemporal fossa. The pterotics are elongate and ventro-medially contain the lateral part of the subtemporal fossa which is a broadly curved depression. The posttemporal fossae (Fig. 7c) are shallower and open into the subtemporal fossae.

Mouth and jaw

Howes (1982) gave a detailed anatomical description of the jaw structure of *Semiplotus semiplotus* and compared it with that of *Onychostoma*, *Varicorhinus*, *Capoeta* and *Cyprinion*. A significant character of the lower jaw in *Semiplotus*, *Cyprinion* and *Scaphiodonichthys* is a synarthritic dentary joint (Fig. 8b). *Onychostoma*, *Scaphesthes*, *Varicorhinus* and *Capoeta* all lack this feature, but in *Onychostoma* and *Scaph-esthes* a strong process stems from the medial symphysial surface and curves posteromedially (Fig. 8a). A thick liga-ment connects the process with its partner. Such a process is
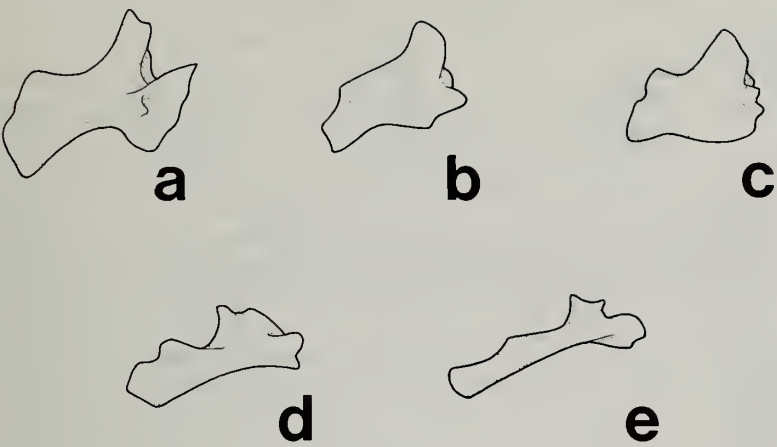
Fig. 5 Dorso-anterior view of the right palatine in:
a. *Onychostoma sima*
b. *Scaphesthes barbatulus*
c. *Scaphiodonichthys burmanicus*
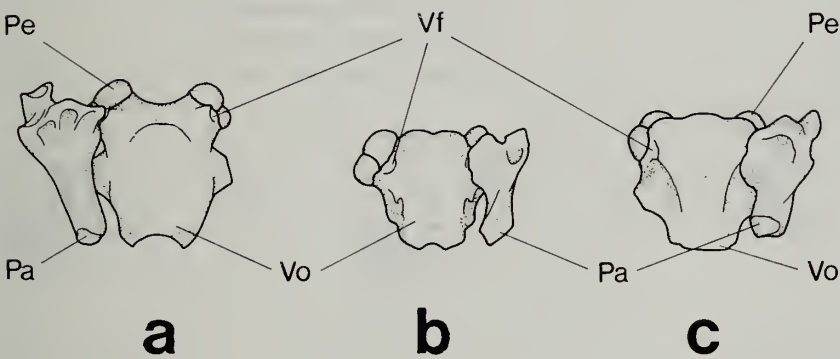d. *Varicorhinus beso*
e. *Barbus barbus*

Fig. 6 Ventral view of vomer and palatine in:
a. *Onychostoma sima*
b. *Scaphiodonichthys burmanicus*
c. *Semiplotus semiplotus*

lacking in *Varicorhinus* and *Capoeta*. In these genera, the dentaries contact one another across a flat symphysial surface and there is no inner ligament (Fig. 8c).

The mouth of *Onychostoma* and *Scaphesthes* exhibits three external morphotypes. In type one (Fig. 9a) the mouth width spans that of the head; this type is present in *Onychostoma sima*, *O. elongatus*, *O. angustistomatus* and *Scaphesthes macrolepis*. In type two (Fig. 9b) the mouth width is greater than that of the head (the corners of the mouth are expanded beyond the lateral margin of the head); it is present in *Scaphesthes barbatulus*, *S. alticorpus*, *S. lepturus* and *Onychostoma gerlachi*. In type three (Fig. 9c) the mouth is moderate to small, its width less than that of the head; this type is present in *Onychostoma lini*, *O. ovalis*, *O. rhomboides* and *Scaphesthes barbatus*. Despite these external differences, all these taxa possess the derived osteological structures of the jaws described for *Onychostoma laticeps* (see above and Howes, 1982).

The mouth of *Scaphiodonichthys* belongs to type two category, but lacks the lateral groove that runs from the snout to the angle of the mouth (Fig. 10) and which is present in *Onychostoma* and *Scaphesthes*. The 1st and 2nd infraorbitals entirely cover the maxilla and premaxilla laterally. The *adductor mandibulae* muscle A_1 inserts on the posterior tip of the maxilla (Fig. 11b). In the majority of cyprinids, including *Onychostoma*, *Scaphesthes*, *Varicorhinus*, *Cyprinion* and *Semiplotus*, the snout groove is present and the *adductor mandibulae* muscle A_1 inserts on a small centrally situated lateral process on the maxilla (Fig. 10 & 11, a,c,d).

Circumorbitals

Although the supraorbital is large in *Onychostoma sima* (Fig. 1 & Fig. 12), it is widely separated anteriorly from the first
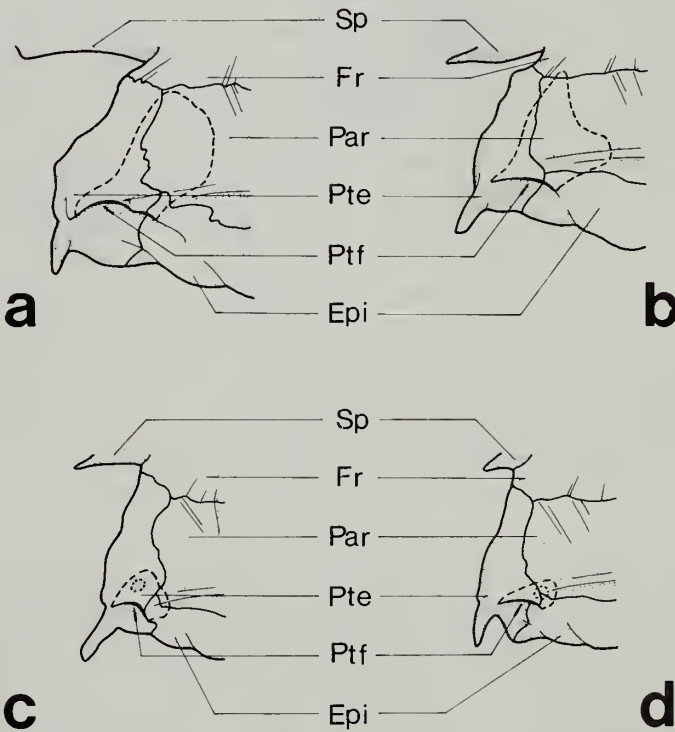

Fig. 7 Pterotic region in dorsal view to show the posttemporal fossa of:
a. *Onychostoma sima*
b. *Scaphiodonichthys burmanicus*
c. *Varicorhinus beso*
d. *Cyprinion watsoni*

infraorbital (lachrymal) and posteriorly from the 5th infraorbital, as in most barbins. The lachrymal is a deep pentagonal bone; its inner face attaching to the mid-lateral ascending
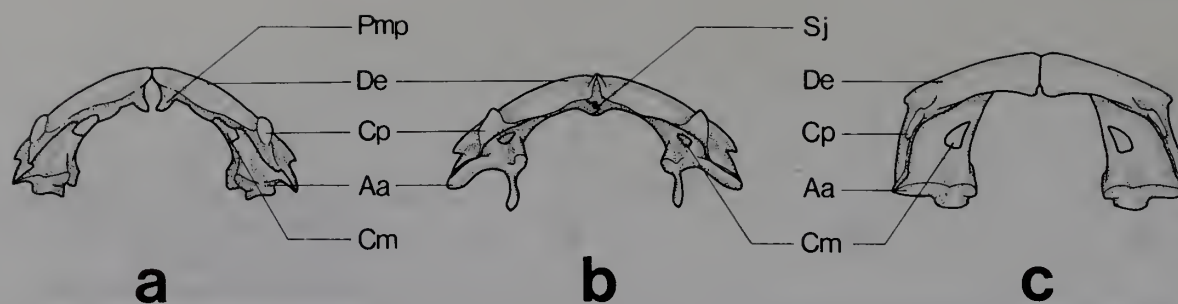
Fig. 8 Lower jaw bones in dorsal view of: a. *Onychostoma sima*; b. *Semiplotus semiplotus*; c. *Varicorhinus beso*.
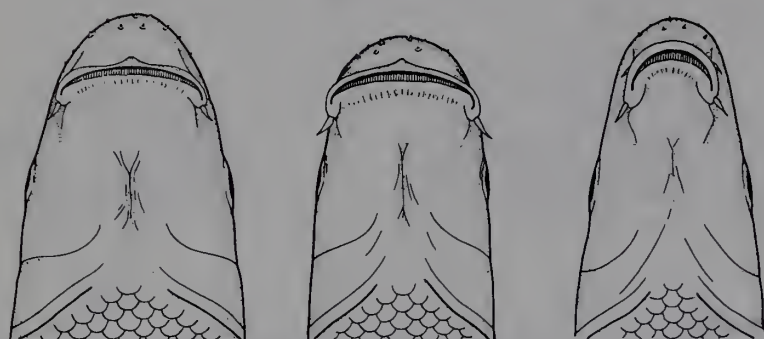

Fig. 9 Ventral view of the heads in:
a. *Onychostoma sima*
b. *Scaphesthes barbatulus*
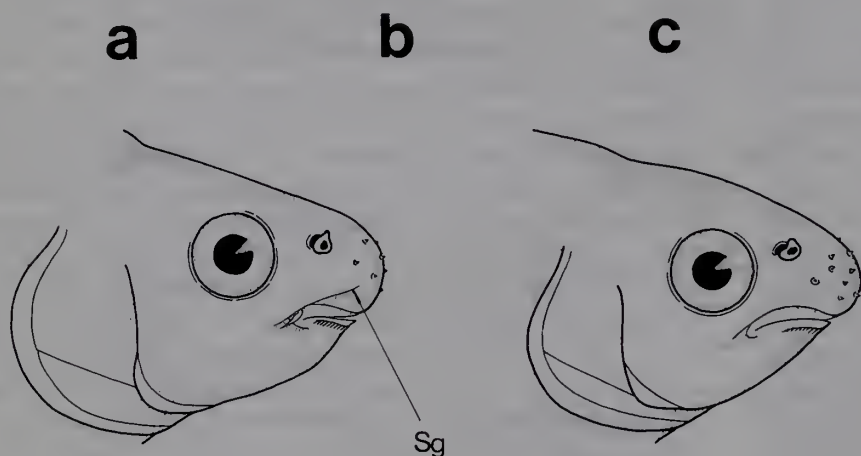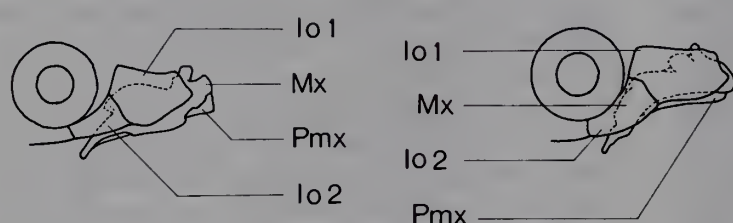c. *Scaphesthes barbatus*

Fig. 10 Lateral view of head and infraorbital bones of:
(left) *Onychostoma sima*
(right) *Scaphiodonichthys burmanicus*

maxillary process *via* tendinous tissue. The sensory canal runs through the ventral part of the lachrymal. The other infraorbitals are narrow and the sensory canal runs along their dorsal rim. The 5th infraorbital is reduced to a bony tube which extends dorso-posteriorly and does not contact the lateral process of the sphenotic. There are thus large gaps between the 5th infraorbital and the sphenotic, and the 5th infraorbital and the opercular process. Almost all of the *dilatator operculi* muscle is exposed. There is also a wide gap between the pterotic and dorsal border of the operculum and the *levator operculi* is well-developed. The condition of the circumorbitals in all species of *Onychostoma* and *Scaphesthes* is the same as described for *O. sima*.

In *Varicorhinus beso* (Fig. 12) the lachrymal is also a deep pentagonal bone but the sensory canal runs centrally through the bone; the anterior part of the sensory canal runs close to the bone's anterior border. The 2nd and 3rd infraorbitals are

shallow but the 4th and 5th infraorbitals are deep. In some species of *Varicorhinus*, e.g. *V. ruwenzorii* (Fig. 13a) and *V. macrolepidotus*, the 4th and 5th infraorbitals are apparently fused (in some specimens of *V. beso* both the 4th and the 5th may be present on one side only). The upper infraorbital is never reduced and contacts the lateral process of the sphenotic and the opercular process. The *dilatator operculi* muscle is almost covered completely by the infraorbital, and the upper gap between the pterotic and the opercular border is very narrow.

The shape of the lachrymal is variable in the barbins (Howes, 1987) and it is difficult to evaluate it as a phylogenetic character. In most barbins (Fig. 13a–j) the 4th infraorbital is not reduced and the 5th infraorbital is never reduced to only the sensory canal and it always contacts the lateral process of the sphenotic. *Cyprinion* and *Semiplotus* (Fig. 13i,j) both possess this morphology, which, from its widespread distribution appears

Table 1 Vertebrae, lateral line scales and branched rays counts in some examined species

| Species	Vertebrae Total	Pre-dorsal	Lateral line scales	Branched rays Dorsal	Anal
Onychostoma sima	44	11	45–48	8	5
O. gerlachi	45	11	46–49	8	5
O. lini	45	11	47–49	8	5
O. rhomboides	42	10	42–45	8–9	5
Scaphesthes barbatulus	44	12	44–47	8	5
S. macrolepis	48	14	50–53	8	5
S. barbatus	45	12	47–48	8	5
S. lepturus	43	11	44–48	8	5
Scaphiodonichthys burmanicus	41	11	37–38	9–10	5
S. acanthopterus	42	11	41–42	11–12	5
S. macracanthus			42–44	13–14	5
Semiplotus semiplotus	38	9	30–31	24–28	8–10
Cyprinion macrostomus	40	11	37–41	13–16	7
C. watsoni	38	11	37–40	9–11	7
C. microphthalmum	37	11	37–40	10–11	7
Varicorhinus beso	42	10	30–35	9–10	5
V. tanganicus	44	12	64–70	8–9	5
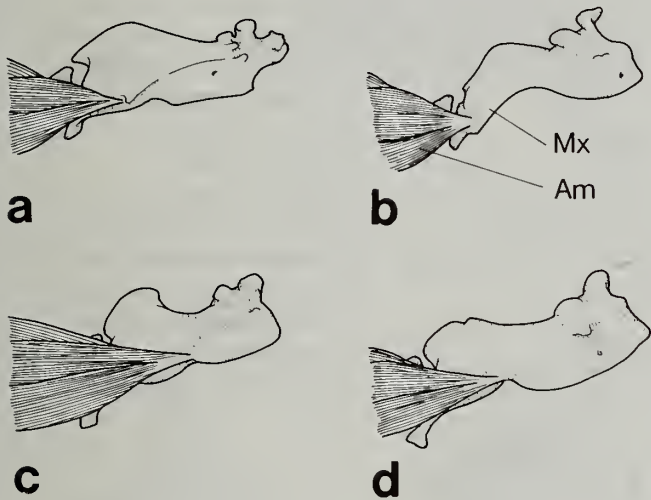
Fig. 11 Insertion of *adductor mandibulae* muscle to upper jaw in:
  a. *Onychostoma sima*
  b. *Scaphiodonichthys burmanicus*
  c. *Cyprinion macrostomus*
  d. *Varicorhinus beso*

to be the plesiomorphic condition. Only *Scaphiodonichthys* and *Schizothorax* (Fig. 13k,l) share the supposedly derived infraorbital morphology of *Onychostoma* and *Scaphesthes*.

Vertebral column and dorsal fin

In *Onychostoma sima* (Fig. 14a) the neural complex is tall and axe-shaped with a forwardly inclined anterior border and widely separated from the supraoccipital as in most barbins. The posterior border of the neural complex is slightly concave and widely separated from the posteriorly inclined 4th neural spine, which is less than a half its height. There are 7 supraneurals between the neural complex and the first dorsal pterygiophore. Each supraneural is a lamellar, triangular, poorly ossified bone narrowly separated from each of those adjacent, their dorsal borders forming an almost continuous bony ridge along the midline of the body. The anterior neural spines are tall and slender.

In *Scaphesthes barbatulus* (Fig. 14b) the neural complex is low with irregular anterior and posterior borders. The 4th

neural spine is short and widely separated from the posterior border of the neural complex. There are 8 stick-like supraneurals of irregular size between the neural complex and the first dorsal pterygiophore.

These two morphotypes of the vertebral column are present in species of *Onychostoma*, *Scaphesthes* and *Cyprinion*. That described for *O. sima* is also found in *O. gerlachi*, *O. rhomboides*, *S. lepturus*, *C. macrostomus* and *C. watsoni*; that for *S. barbatus* is also found in *S. macrolepis* and *O. lini*.

Howes (1982) described the anterior vertebral column of *Semiplotus semiplotus* and *Scaphiodonichthys burmanicus*. In the former, the supraneurals are enlarged, articulating with each other and overlapping the neural complex and the first dorsal pterygiophore. In the latter taxon (Fig. 14c) the supraneurals are also sequentially joined and overlap the anterior margin of the 1st dorsal pterygiophore. The anterior margins of the neural spines are produced to form a flange which articulates with the base of each supraneural.

In *Varicorhinus beso* (Fig. 14d) the neural complex is also tall and axe-shaped as *Onychostoma sima*, but the 4th neural spine is vertically inclined and close to the posterior border of the neural complex. There are only six supraneurals which are enlarged and articulate with one another, the last element contacts the 1st dorsal pterygiophore.

In the Cyprininae, the vertebral number is variable, with a modal range of 38–40 (Howes, 1987). However, the total vertebral number of *Onychostoma* and *Scaphesthes* is 42–48 and is higher than that of most barbins, but the pre-dorsal vertebral number is only 10–12 (with the exception of *Scaphesthes macrolepis* which has 14). The lateral line scales number 42–53. In *Scaphiodonichthys*, *Semiplotus* and *Cyprinion*, the total number of the vertebrae and the lateral line scales are all lower than those of *Onychostoma* and *Scaphesthes*, but the number of predorsal vertebrae is similar in all genera. In view of its restricted distribution, I consider a high total number of vertebrae as a synapomorphy for *Onychostoma* and *Scaphesthes* (Table 1).

The number of the dorsal and anal fin rays is stable in *Onychostoma* and *Scaphesthes* (Table 1). There are 8–9 branched dorsal fin rays and 5 branched anal fin rays in these two genera which are the plesiomorphic numbers for cyprinines. In *Scaphiodonichthys*, *Semiplotus* and *Cyprinion*,
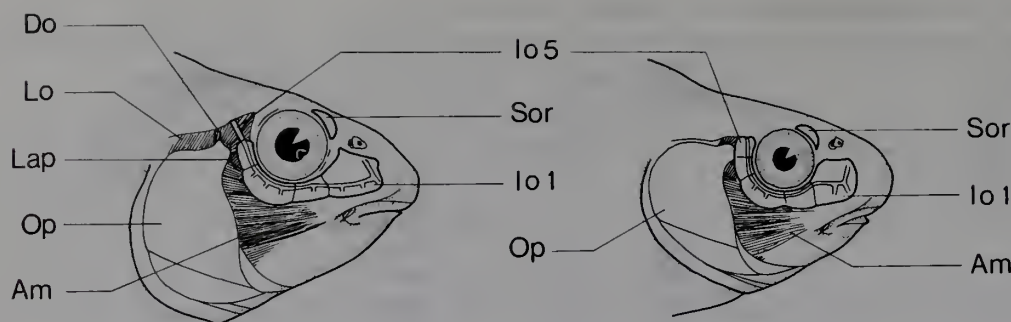
Fig. 12 Circumorbital series of:
(left) *Onychostoma sima*
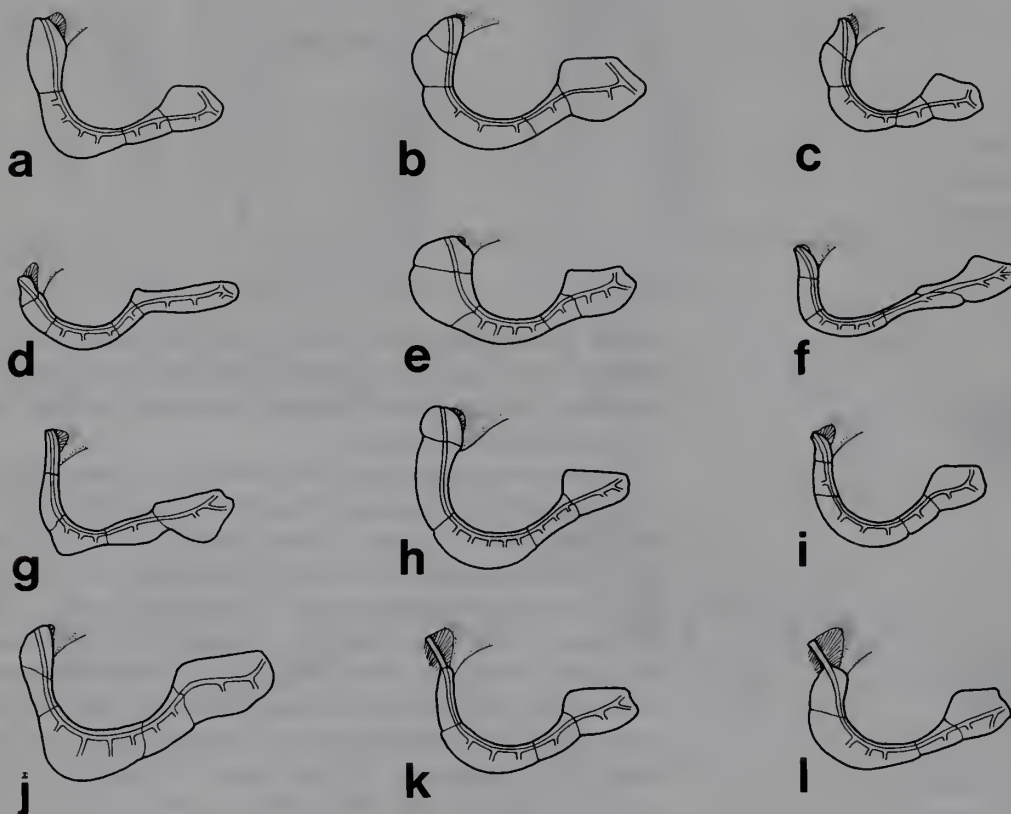(right) *Varicorhinus beso.*

Fig. 13 Infraorbital series of:
a. *Varicorhinus ruwenzorii*
b. *Varicorhinus albpinnis*
c. *Capoeta capoeta*
d. *Barbus barbus*
e. *Barbus luteus*
f. *Labeo cylindricus*
g. *Garra quadrimaculatus*
h. *Cirrhina jullieni*
i. *Cyprinion macrostomus*
j. *Semiplotus semiplotus*
k. *Scaphiodonichthys burmanicus*
l. *Schizothorax richardsoni.*

however, the number of the rays of the dorsal or anal fin is higher and variable (Table 1) and is considered an apomorphic condition.

In the Cyprininae, the last unbranched dorsal fin ray varies from being flexible to heavily ossified and may be smooth or serrated along its posterior margin. This condition is also found in *Cyprinion* (including *Semiplotus* and *Scaphiodonichthys*). Whereas in *Varicorhinus* the posterior margin of the last unbranched dorsal fin ray is smooth, it may be also flexible or heavily ossified. Although the posterior margin of the last unbranched dorsal fin ray is serrated in *Onychostoma*, the ray is more or less flexible and segmented; it is never fully ossified. In some species, *Onychostoma lini*, the last unbranched dorsal fin ray is slender and serrations are not apparent (Fig. 15).

DISCUSSION

Phylogenetic position of the genus *Onychostoma*

From the foregoing descriptions and analyses, no synapomorphic characters can be found in *Onychostoma* (including *Scaphesthes*) and *Varicorhinus* except the possession of a

sharp, horny edge to the lower jaw. Howes (1982) regarded this feature in both taxa as a parallelism. *Varicorhinus* possesses many plesiomorphic characters in common with *Barbus* sensu lato; although Howes (1982) has suggested that *Varicorhinus* forms a close relationship with African *Barbus*.

Characters identified as apomorphic in *Onychostoma* also occur in *Scaphesthes*, *Scaphiodonichthys*, *Semiplotus* and *Cyprinion*. The synapomorphies which serve to identify these taxa as a monophyletic group are:
1. Supraethmoid broad and short, its rostral process ventrally directed; the medial part of the dorsal surface depressed and covered with a thick connective tissue.
2. Vomer provides a facet articulating with the short and compressed palatine.
3. Parietal and prootic short and deep almost rectangular.
4. Pterotic short and broad, ventrally containing the lateral part of the subtemporal fossa as a U-shaped depression.
5. Subtemporal fossa is ellipsoidal and deep.

Howes (1982) identified a series of synapomorphic characters possessed by *Cyprinion*, *Semiplotus* and *Scaphiodonichthys* and thus treated these taxa as a single genus, *Cyprinion*. The principal synapomorphy is the presence of a synarthritic dentary joint. *Onychostoma* and *Scaphesthes* both lack this significant feature, but possess a strong medial, posteriorly directed process on the symphysial surface of the dentary.
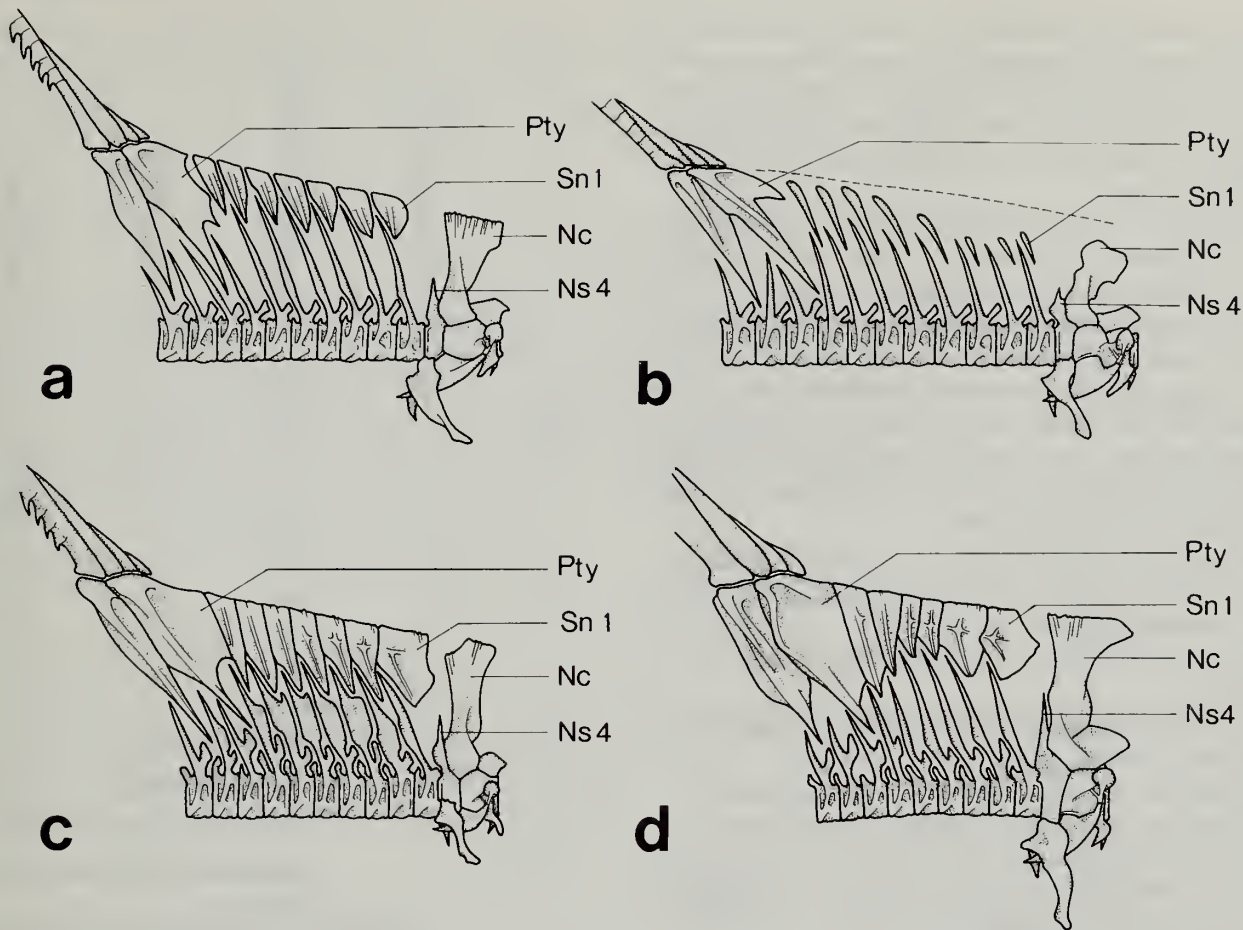
Fig. 14 Anterior vertebral column of: a. *Onychostoma sima*; b. *Scaphesthes barbatulus*; c. *Scaphiodonichthys burmanicus*; d. *Varicorhinus beso*.
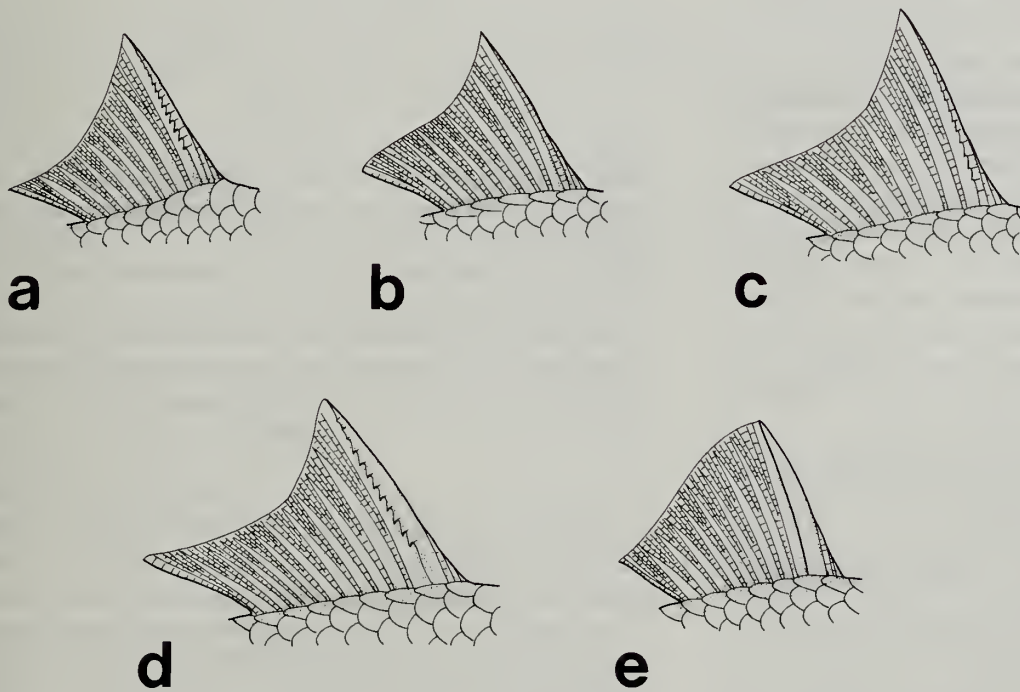

Fig. 15 Dorsal fins of:
a. *Onychostoma sima*
b. *Scaphesthes barbatulus*
c. *Onychostoma lini*
d. *Scaphiodonichthys burmanicus*
e. *Varicorhinus beso*.

This feature is not found in other 'sector mouth' taxa and is thus identified as an apomorphic character.

Scaphiodonichthys possesses a series of autapomorphic characters: it lacks a snout groove; the 1st and 2nd infraorbitals cover the maxilla and the premaxilla; the *adductor mandibulae* muscle inserts on the posterior tip of the maxilla and the pre-dorsal neural spines are extended. There are two characters shared by *Onychostoma* and *Scaphiodonichthys*, one of which is the reduced 5th infraorbital; the other is the anal fin with 5 branched rays. The latter is a plesiomorphic character in cyprinines, but the former is an apomorphic

character restricted to these two taxa. However, in view of the conflicting nature of other synapomorphies which support the monophyly of *Scaphiodonichthys*, *Semiplotus* and *Cyprinion* it would appear that this character is homoplastic.

Semiplotus shares many apomorphies with *Cyprinion* and *Scaphiodonichthys* and possesses several autapomorphies (Howes, 1982). It also shares with both *Scaphiodonichthys* and *Onychostoma* a deep posttemporal fossa. It may be argued that since this character is present in all three taxa but absent in *Cyprinion* it has been lost in that genus. However, since it appears that *Cyprinion* is the plesiomorphic member

of the triad of *Cyprinion*, *Semiplotus* and *Scaphiodonichthys* then it would presumably possess this feature in one or more of its derived species. As it does not, I apply the more parsimonious argument that it too is a homoplasy between, on the one hand *Semiplotus* and *Scaphiodonichthys*, and on the other *Onychostoma*.

Howes (1982) preferred to regard *Scaphiodonichthys* and *Semiplotus* as synonyms of *Cyprinion*, but was unable to determine the sister-group relationship of *Cyprinion*. It is clear that this lineage is *Onychostoma*, but since this genus shares some of those features which are distributed amongst '*Cyprinion*', it appears taxonomically justifiable to regard *Scaphiodonichthys*, *Semiplotus* and *Cyprinion* of equal (generic) rank. The alternative would be to include *Onychostoma* within *Cyprinion* but this then would not adequately reflect the relationships of the taxa (Fig. 16).

The following characters are identified as synapomorphies for all species of *Onychostoma* and *Scaphesthes*:
1. Vertebral number is 42–48.
2. A strong posteromedial process on the symphysial surface of the dentary.
3. The 5th infraorbital is reduced to a sensory canal and does not contact the sphenotic.
4. Posttemporal fossa is deep and extends to the frontal.

From the foregoing analyses, I consider *Onychostoma* and *Scaphesthes* to be a monophyletic group whose relationship is remote from *Varicorhinus*, but close to *Cyprinion*. I recognize it as the sister-group of the assemblage comprising *Cyprinion*, *Semiplotus* and *Scaphiodonichthys*.

Classification and phyletic relationships within *Onychostoma*

Although at times *Onychostoma* has been regarded as a synonym of *Varicorhinus* all previous authors have recognized it to contain two groups. These groups have been regarded as subgenera *Onychostoma* and *Scaphesthes* (or *Gymnostomus*). The former includes species possessing an osseous and serrated last simple dorsal fin ray, whereas the latter includes those having a flexible and smooth ray. Parenthetically, it should be noted that *Scaphesthes* should be used in preference to *Gymnostomus*, the type species of which, *G. ariza*, has been referred to the genus *Labeo* (Jayaram, 1981).

A comparison between the type species of *Onychostoma* and *Scaphesthes* reveals the following differences:
1. In *Onychostoma sima* the last simple dorsal ray is serrated, but is smooth in *Scaphesthes barbatulus*.
2. In *Onychostoma sima* the mouth width is equal to the head width. In *Scaphesthes barbatulus* the mouth is very wide being greater than the head width.
3. In *Onychostoma sima* the neural complex is tall and axe-shaped; there are 7 triangular supraneurals between the neural complex and the first dorsal pterygiophore. In *Scaphesthes barbatulus* the neural complex is low and there are 8 stick-shaped supraneurals anterior to the dorsal fin.

These three character complexes are, however, irregularly distributed among the species of *Onychostoma* and *Scaphesthes*, and thus cannot be used as diagnostic for either of the two groups.

The last simple dorsal fin ray is never really ossoeus in *Onychostoma*, it is always segmented and flexible at its tip. In *Onychostoma lini* the ray is serrated, but is as slender as that in *Scaphesthes barbatulus*. The use of serrated simple dorsal
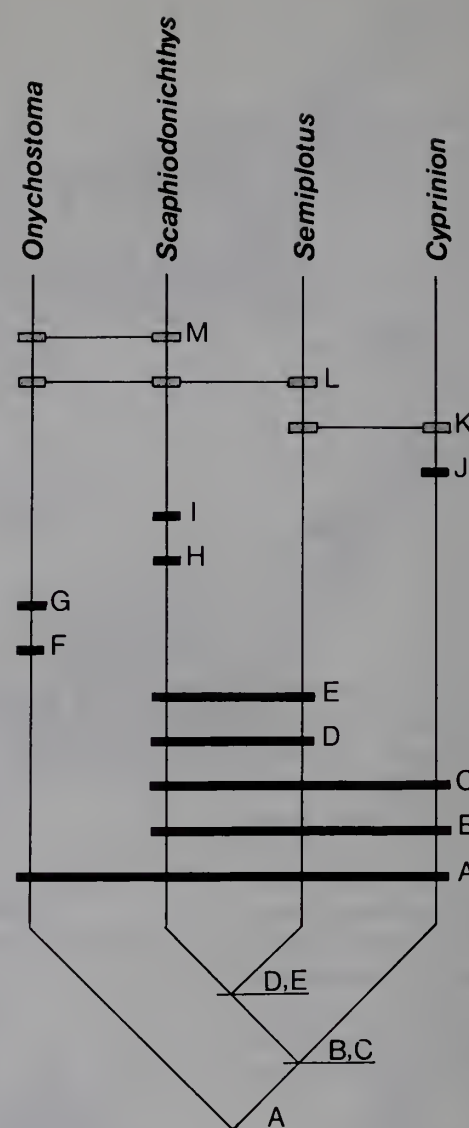

Fig. 16 Cladogram of relationships and apomorphic characters distribution in the *Onychostoma-Cyprinion* group. Level: A. cranial synapomorphies (see text p. 116); B. synarthritic dentary joint; C. branched rays of the dorsal fin; D. jaw synapomorphies (see Howes, 1982); E. cranial synapomorphies (see Howes, 1982); F. medio-dorsal process of dentary; G. vertebral number; H. mouth apomorphies; I. extended neural spines; J. expanded pelvic fin rays; K. branched ray of the anal fin; L. posttemporal fossa; M. tubed 5th infraorbitial.

fin rays as a synapomorphy for *Onychostoma* is thus not justified. According to this character the division of *Onychostoma* into two subgenera is not supported.

The shape of the neural complex and supraneurals are variable within the Cyprinidae (Howes, 1987). In *Onychostoma* species the development of this character complex is equally variable and it is difficult to evaluate which state of this character is apomorphic. I therefore regard *Scaphesthes* as a junior synonym of *Onychostoma*.

The width of the mouth appears to be a more significant character in diagnosing the genus. On the basis of the various morphotypes (see p. 113) *Onychostoma* species can be placed in three subgroups. Table 2 compares morphological features of all *Onychostoma* species and Figure 17 shows their suggested interrelationships. The polarity of most of these characters cannot be evaluated, thus the scheme presented is classificatory rather than phylogenetic.

Table 2. Comparison of some characters in species of *Onychostoma*. Data presented from Wu *et al.* (1977) and Bǎnǎrescu (1971)

Species of Onychostoma	Mouth	Lateral line scales	Barbels	Last simple dorsal ray	Neural complex	Caudal peduncle depth in body length	Caudal peduncle depth in its length
barbata				slender and smooth			
lini		47–50	present	slender and serrated	low	10.0–12.1	1.5–1.9
elongata			absent in adult	strong and serrated		12.6–13.5	3.0
ovalis	slightly narrow					6.8–8.0	1.2–1.5
rhomboides		42–45	present	strong and serrated	tall		
rara						7.9–8.8	1.4–1.7
macrolepis		50–53	present	slender and smooth	low		
sima			absent in adult		tall		
angustistomata	moderate			strong and serrated		8.1–10.1	1.3–1.7
brevis			present	slender and serrated			
barbatula		44–49	present		low		
alticorpus				slender and smooth		9.1–10.1	1.7–1.8
leptura	wide		absent				
gerlachi			absent in adult	strong and serrated	tall	11.4–14.1	2.0–2.8

A synopsis of *Onychostoma* species

Onychostoma Günther, 1896
   Onychostoma Günther, 1896
   Scaphesthes Oshima, 1919
   Scaphiodontella Oshima, 1920
TYPE SPECIES. *Onychostoma laticeps* Günther = *O. sima* (Sauvage & Dabry).

Onychostoma sima (Sauvage & Dabry, 1874)
   Barbus (*Systomus*) *simus* Sauvage *et* Dabry, 1974: 8.
   Onychostoma laticeps Günther, 1896: 211.
DISTRIBUTION. Upper reaches of the Yangtze River and the Pearl River.

Onychostoma angustistomata (Fang, 1940)
   Varicorhinus angustistomata Fang, 1940: 139.
   Varicorhinus szechwanensis Chang, 1944: 44.
DISTRIBUTION. Upper reaches of the Yangtze River.

Onychostoma brevis (Wu & Chen, 1977)
   Varicorhinus (*Onychostoma*) *brevis* Wu & Chen, 1977: 318.
DISTRIBUTION. Upper reaches of the Yangtze River.

Onychostoma macrolepis (Bleeker, 1871)
   Gymnostomus macrolepis Bleeker, 1871: 32.
   Varicorhinus shansiensis Nichols, 1925: 2.

DISTRIBUTION. The Haihe River, Yellow River and Yangtze River.

Onychostoma barbata (Lin, 1931)
   Gymnostomus barbatus Lin, 1931: 113.
DISTRIBUTION. Upper reaches of the Pearl River.

Onychostoma lini (Wu, 1939)
   Varicorhinus lini Wu, 1939: 103.
DISTRIBUTION. Upper reaches of the Pearl River and the Yuanjiang River (a tributary of the Yangtze River).

Onychostoma elongata (Fang, 1940)
   Varicorhinus elongatus Fang, 1940: 138.
DISTRIBUTION. Upper reaches of the Pearl River.

Onychostoma ovalis Pellegrin & Chevey, 1936
   Onychostoma ovalis Pellegrin & Chevey, 1936: 22.
DISTRIBUTION. The Red River.

Onychostoma rhomboides (Tang, 1942)
   Varicorhinus rhomboides Tang, 1942: 156.
DISTRIBUTION. The Pearl River and the Wujiang River (a tributary of the Yangtze River).

Onychostoma rara (Lin, 1933)
   Varicorhinus rarus Lin, 1933: 204.

Fig. 17 Dendrogram of *Onychostoma* species based the distribution of the characters listed in Table 2.

DISTRIBUTION. The Pearl River and the Yuanjiang River (a tributary of the Yangtze River).

Onychostoma barbatula (Pellegrin, 1908)
   Gymnostomus barbatulus Pellegrin, 1908: 263.
   Scaphesthes tamusuiensis Oshima, 1919: 209.
   Varicorhinus robustus Nichols, 1925: 2.
DISTRIBUTION. Fujian, Zhejiang and Taiwan Island.

Onychostoma alticorpus (Oshima, 1920)
   Scaphiodontella alticorpus Oshima, 1920: 126.
DISTRIBUTION. Taiwan Island.

Onychostoma leptura (Boulenger, 1899)
   Gymnostomus lepturus Boulenger, 1899: 961.
DISTRIBUTION: Hainan Island.

Onychostoma gerlachi (Peters, 1880)
   Barbus gerlachi Peters, 1880: 1034.
   Onychostoma vietnamensis Bănărescu, 1971: 244.
DISTRIBUTION. The Pearl River, the Red River and Hainan Island.

Biogeography of the genus *Onychostoma*

As mentioned above, *Onychostoma* is the sister-group of the complex comprised of *Scaphiodonichthys*, *Semiplotus* and *Cyprinion*. Together these genera form a monophyletic assemblage named as the *Onychostoma-Cyprinion* group. This group is distributed from southeast China, Thailand and Laos, south of Himalaya, to the Arabian Peninsula in the west. Taki (1975) has suggested some dispersal routes to explain the distribution of the *Onychostoma*-group (including *Onychostoma*, *Scaphiodonichthys*, *Scaphiognathops*, *Semiplotus* and *Scaphiodon*). However, it is suggested that the upheaval of the Tibetan Plateau and the Yunnan Plateau before the Pliocene and the presence of pockets of the Tethys Sea during the Pliocene made such dispersal impossible. I consider that the ancestral lineage of the *Onychostoma-Cyprinion* group had been widely distributed throughout central and southern Asia and the vicariant events of plateau formation disrupted this distribution, the consequence being the resultant taxa.

No definitive fossil *Onychostoma* has been found, but many fossil barbin fishes are known from the Miocene from sites in central and eastern Asia. The relationships of these fossils have not been determined and the representative of the ancestral lineage of the *Onychostoma-Cyprinion* group is possibly among them. Among present species of this group, *Onychostoma macrolepis* possesses a number of plesiomorphic characters. For example, the last simple dorsal fin ray is slender and smooth, the dorsal branched rays number 8, the anal 5; the neural complex is low and the supraneurals are stick-like; the mouth is moderate in width and barbels are present. This species occurs in the most northern part of the geographical range of the group. It occurs in the mountain streams of the Haihe River, the Yellow River and the Yangtze River. On account of the cold climate the fish hibernates in burrows from October to April. I consider *Onychostoma macrolepis* to be a relic of the ancestral lineage of the *Onychostoma-Cyprinion* group and assume this lineage to have been widespread in central and eastern Asia before the Pliocene when warmer climates prevailed in this area.

Since the late Tertiary the climate has cooled and the fishes of *Onychostoma-Cyprinion* group supposedly became extinct in the northern part of central and eastern Asia. Some of them may have migrated towards southern Asia following the close of the Tethys Sea. The upheaval of the Tibetan Plateau

(including the Yunnan Plateau) forms a barrier between south-western Asia and eastern Asia which would have split the group into two subgroups. The eastern subgroup, *Onychostoma*, never occurs westward beyond the Yunnan Plateau and the Red River. The Yunnan Plateau appears to form a boundary between southern Chinese and south-eastern Asian taxa of many groups.

The three subgroups of *Onychostoma* species occupy restricted areas; the moderate-mouth (the mouth width spans that of the head) group is confined to the north of the Nanling Mountain Range; the narrow-mouth group to the west of south China and the wide-mouth group to the east of south China. A half of the species of *Onychostoma* are found in the Pearl River system, which suggests that Pearl River system has been the evolutionary centre of *Onychostoma*.

As yet the relationships of the *Onychostoma-Cyprinion* group to other cyprinines remains unresolved.

REFERENCES

Bănărescu, P. 1971. A review of the species of the subgenus *Onychostoma s. str.* with description of a new species (Pisces, Cyprinidae). *Revue Roumaine de Biologie*, Zool. 16(4): 241–248.
—— 1971. Revision of the *Onychostoma*—subgenus *Scaphesthes* (Pisces, Cyprinidae). *Revue Roumaine de Biologie*, Zool. 16(6): 357–364.
Bleeker, P. 1871. Mémoire sur les Cypriniodes de China. *Verhandelingen der Koninklijke Akademie van Wetenschappen. Amsterdam.* Afdeeling Natuurkunde 12: 1–91.
Boulenger, G. A. 1899. On the reptiles, batrachians and fishes collected by the late Mr. John Whitehead in the interior of Hainan. *Proceedings of the Zoological Society of London*: 956–962.
Chang, H. W. 1944. Notes on the fishes of Western Szechwan and Eastern Sikang. *Sinensia* 15 (1–6): 27–60.
Chen, X. L., Yue, P. Q. & Lin, R. D. 1984. Major groups within the Family Cyprinidae and their phylogenetic relationships. *Acta Zootaxonomica Sinica* 9 (4): 424–440.

Fang, P. W. 1940. Deux nouvelles espèces de cyprinidés de Chine appartenant au sous-genre *Onychostoma* Gunther. *Bulletin de la Société Zoologique de France*, Paris 65: 138–140.
Günther, A. 1896. Report on the collections of reptiles, batrachians and fishes made by Messrs. Potanin and Berezowski in the Chinese provinces Kansu and Szechuan. *Annuaire du Musée Zoologique de l'Académie Imperiale des Sciences*. St. Petersburg 1 : 199–219.
Howes, G. J. 1982. Anatomy and evolution of the jaws in the semiplotine carps with a review of the genus *Cyprinion* Heckel, 1843 (Teleostei: Cyprinidae). *Bulletin of the British Museum (Natural History)*. (Zool.) 42 (4): 299–355.
—— 1982. The phylogenetic position of the Yugoslovian cyprinid fish genus *Aulopyge* Heckel, 1841, with an appraisal of the genus *Barbus* Cuvier & Cloquet, 1816 and the subfamily Cyprininae. *Bulletin of the British Museum (Natural History)*. (Zool.) 52 (5): 165–196.
Jayaram, K. C 1981. *The Freshwater Fishes of India, Pakistan, Bangladesh, Burma and Sri Lanka*. Calcutta.
Lin, S. Y. 1931. *Carps, and Carp-like Fishes of Kwangtung and Adjacent Provinces*. Canton.
—— 1933. Contribution to a study of Cyprinidae of Kwangtung and adjacent provinces, 2. *Lingnan Science Journal* 12 (2): 199–215.
Mirza, M. R. 1975. Freshwater fishes and zoogeography of Pakistan. *Bijdragen tot de Dierkunde* 45 (2): 143–180.
Nichols, J. T. 1925. Some Chinese fresh-water fishes. VII. New carps of the genera *Varicorhinus* and *Xenocypris*. *American Museum Novitates* (182): 1–8.
—— 1943. *Freshwater Fishes of China*. Natural History of Central Asia 9. American Museum of Natural History, New York.
Oshima, M. 1919. Contribution to the study of the fresh-water fishes of the Island of Formosa. *Annals of the Carnegie Museum* 12: 169–382.
—— 1920. Notes on freshwater fishes of Formosa, with descriptions of new genera and species. *Proceedings of the Academy of Natural Sciences of Philadelphia* 72: 120–135.
Pellegrin, J. 1908. Poissons d'eau douce de Formosa, description d'une espèce nouvelle de la Famille des Cyprinidés. *Bulletin du Muséum National d'Histoire Naturelle*. Paris 14: 263.
—— and Chevey, P. 1936. Cyprinides nouveaux du Tonkin. *Bulletin de la Société Zoologique de France*. Paris 61: 18–27.
Peters, W. 1880. Über eine Sammlung von Fischen, welche Hr. Dr. Gerlach in Hongkong gesandt hat. *Monatsberichte der Koniglichen Preussischen Akademie der Wissenschaften zu Berlin*: 1029–1037.
Sauvage, H. E. & Dabra de Thiersant 1874. Notes sur les poissons des eaux douces de Chine. *Annales des Sciences Naturelles*. Paris Zool., ser. 6, 1 (5): 7–14.
Smith, H. M. 1945. The freshwater fishes of Siam, or Thailand. *Bulletin of the United States National Museum* (188): 1–622.
Taki, Y. 1975. Cyprinid fishes of the genera *Onychostoma* and *Scaphiodonichthys* from upper Laos, with remark on the dispersal of the genera and their allies. *Japanese Journal of Ichthyology* 22 (3): 143–150.
Tang, D. S. 1942. Fishes of Kweiyang, with description of two new genera and five new species. *Lingnan Science Journal* 20 (2–4): 147–166.
Wu, H. W. 1939. On the fishes of Li-Kiang. *Sinensia* 10 (1–6): 92–142.
Wu, H. W. *et al*. 1977. *The Cyprinid Fishes of China*. 2. Shanghai.